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Supplementary Material

Multitaper spectral analysis

Here we present modern multitaper methods of spectral analysis used in this paper. These methods were introduced in Thomson (1982) and have been succesfully applied to neurobiological data in recent work[1–3]. Multitaper methods involve the use of multiple data tapers for spectral estimation. A variety of tapers can be used, but an optimal family of orthogonal tapers is given by the prolate spheroidal functions or Slepian functions. These are parameterized by their length in time, T, and their bandwidth in frequency, W. For each choice of T and W, up to K=2TW-1 tapers are concentrated in frequency and suitable for use in spectral estimation[4].

The ordinary continuous-valued time series and point processes are considered in this work form a hybrid data set and spectral analysis provides a unified framework for their analysis. For the ordinary time series consider a continuous-valued process, $x_t; t = 1, \ldots, N$. The basic quantity for further analysis is the windowed Fourier transform, $\tilde{x}_k(f)$:

$$\tilde{x}_k(f) = \sum_{t=1}^{N} w_t^{(k)} x_t e^{-2\pi i f t}$$

$w_t^{(k)}; k = 1, \ldots, K$ are K orthogonal taper functions.

For the point process, consider a sequence of event times $t_j, j = 1, \ldots, N$ in the interval $[0, T]$. These times can be analyzed as a sequence of spike counts, dN(t), called the counting process where the number of events in a short time interval, $[t, t + dt]$, are specified. Here, dt is chosen to be 1ms so up to one event occurs each interval. The spectrum of spike counts leads to the spike spectrum.

The quantity for further analysis of the counting process is the windowed Fourier transform of the spike counts, denoted by $d\tilde{N}_k(f)$:

$$d\tilde{N}_k(f) = \sum_{j=1}^{N} w_{t_j}(k) e^{-2\pi i f t} - \frac{N(T)}{T} \tilde{w}_k(0)$$

$\tilde{w}_k(0)$ is the Fourier transform of the data taper at zero frequency and N(T) is the total number of spikes in the window.

For continuous processes and counting processes, the multitaper estimates for the spectrum $S_X(f)$, cross-spectrum $S_{XY}(f)$ and coherency $C_{XY}(f)$ are given by:

$$S_X(f) = \frac{1}{K}\sum_{k=1}^{K}\left|\tilde{x}_k(f)\right|^2$$

$$S_{XY}(f) = \frac{1}{K}\sum_{k=1}^{K}\tilde{y}_k(f)\tilde{x}_k^*(f)$$

$$C_{XY}(f) = \frac{S_{XY}(f)}{\sqrt{S_X(f)S_Y(f)}}$$

The auto- and cross-correlation functions can be obtained by inverse Fourier transforming the spectrum and cross-spectrum.

Each estimate contains 2K degrees of freedom when performed on a single trial. When averaging over trials we introduce an additional index, i, denoting trial number, $\tilde{x}_{k,i}(f)$. This increases the number of degrees of freedom for each estimate by a factor equal to the number of trials in the trial average.

Intuition on application of multitaper methods

An important advantage of the multitaper method is that it offers a natural way of estimating error bars corresponding to most quantities obtained in time series analysis. The fundamental notion is of a local frequency ensemble. If the spectrum of the process is locally flat over a bandwidth 2W then the tapered Fourier transforms, $\tilde{x}_k(f)$, constitute a statistical ensemble for the Fourier transform of the process. Assuming that the underlying process is locally white in the frequency range $[f_0 - W, f_0 + W]$, then it follows from the orthogonality of the data tapers that $\tilde{x}_k(f)$ are uncorrelated random variables with the same variance. For large N, $\tilde{x}_k(f)$ may be assumed to be asymptotically normally distributed under some general circumstances (for related results see Mallows (1967)[5]. Therefore a way of thinking about multitaper estimates is that they are an average over the local frequency ensemble.

Jackknife error bars for multitaper estimates

By using the local frequency ensemble one can also estimate jackknife error bars for the spectra and the above quantities. The idea of the jackknife is to create different estimates by leaving out a data taper in turn. This creates a set of estimates from which a variance may be computed[6]. The variance can be used to test for the difference in means using a t-test[7]. Jackknife error bars for spectral estimates averaged across trials can be generated in the same way from the joint ensemble indexed by trial and taper, $\tilde{x}_{k,i}(f)$.

Advantages over correlation functions

Spectral quantities are estimated in the frequency domain and while they are mathematically equivalent to correlation functions their statistical properties are better understood theoretically and better estimated (for a review see Jarvis and Mitra (2001)[8]).

The problems of estimation bias and variance are controlled by using multitaper spectral analysis. The use of Slepian functions as data tapers controls bias while the use of multiple tapers on the same data controls variance. Other advantages of working in the frequency domain are that i) weak non-stationarity only manifests itself in the spectrum at low frequencies; ii) nearby points in frequency are statistically independent resulting in local error bars for the estimates; and iii) the problem of the normalization of the cross-correlation function is addressed by using the coherency which is dimensionless.

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